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Published in:
Mycological Progress

Link to article, DOI:
10.1007/s11557-016-1227-3

Publication date:
2016

Document Version
Publisher's PDF, also known as Version of record

Mycol Progress (2016) 15:1041–1056
DOI 10.1007/s11557-016-1227-3

ORIGINAL ARTICLE

Four novel *Talaromyces* species isolated from leaf litter from Colombian Amazon rain forests

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Received: 29 April 2016 / Accepted: 7 September 2016 / Published online: 22 October 2016

Abstract Various *Talaromyces* strains were isolated during a survey of fungi involved in leaf litter decomposition in tropical lowland forests in the Caquetá and Amacayacu areas of the Colombian Amazon. Four new *Talaromyces* species are described using a polyphasic approach, which includes phenotypic characters, extrolite profiles and phylogenetic analysis of the internal transcribed spacer region (ITS) barcode, and beta-tubulin (*BenA*) and calmodulin (*CaM*) gene regions. *Talaromyces amazonensis* sp. nov., *T. francoae* sp. nov. and *T. purgamentorum* sp. nov. belong to *Talaromyces* section *Talaromyces*, and *T. columbiensis* sp. nov. is located in section *Bacillispori*. The new species produce several bioactive compounds: *T. amazonensis* produces the potential anticancer agents duclauxin, berkelic acid and vermicillin, and *T. columbiensis* produces the effective anticancer agent wortmannin (together with duclauxin). In addition to the new species, *T. aculeatus* and *T. macrosporus* were isolated during this study on leaf litter decomposition.

Keywords Taxonomy · Phylogeny · Bioactive compounds · Plant biomass degradation

Section Editors: Pedro W. Crous and Roland Kirschner

This article is part of the Special Issue "Biodiversity of Hyphomycetes—Special Issue in honor of Dr. Subramanian".

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Introduction

Fungi play an important role in forest ecosystems, as they are involved in processes such as decomposition of leaf litter. Leaf decomposition contributes to nutrient cycling, in which a large proportion of nutrients from net primary production is returned to the forest floor (Maggs 1985). A number of papers have recently been published on fungal biodiversity in the Colombian Amazon region, reporting new species and new registers. Studies in this region revealed 248 species of macrofungi, but a large number of collections have remained unidentified (López-Quintero et al. 2012; Vasco-Palacios and Franco-Molano 2013). Several new taxa of micro- and macrofungi have been published—for instance, new species of *Penicillium* and *Trichoderma* (Houbraken et al. 2011; López-Quintero et al. 2013; Vasco-Palacios and Franco-Molano 2013; Vasco-Palacios et al. 2014).

Talaromyces species have a worldwide distribution and are isolated from a wide range of substrates. The genus was initially described for teleomorphic species with a *Penicillium* or Penicillium-like anamorph that produces soft-walled ascomata covered by interwoven hyphae. Based on phylogenetic, phenotypic and extrolite data, and following the concept of single-name nomenclature, Samson et al. (2011) transferred all accepted species of *Penicillium* subg. *Biverticillium* to *Talaromyces*. The *Talaromyces* monograph of Yilmaz et al.

(2014) covered 88 species, and the genus currently includes 103 species (Visagie et al. 2015; Romero et al. 2016; Wang et al. 2016; Yilmaz et al. 2016).

Numerous microfungi were isolated from decomposing leaf litter as part of a project to investigate their diversity and their role in the regeneration process of tropical lowland forests. Barcoding using ITS sequences (Schoch et al. 2012) revealed the presence of several *Talaromyces* species, and their taxonomic status is the subject of this report. Four new species are proposed and described using a polyphasic taxonomy, which includes phenotypic characters, analysis of extrolites and multiple gene phylogenies of internal transcribed spacer region (ITS), beta-tubulin (*BenA*) and calmodulin (*CaM*) gene regions.

Material and methods

Strains

The strains were isolated from leaf litter as described in Houbraken et al. (2011). In short, small particles from fresh or 4–6 month-old leaf litter were washed and placed on 2 % water agar. The strains were obtained from three forests in Colombia Amazonia, namely mature forests in Araracuara (Middle Caquetá) and Amacayacu (Amazonas), and a *Pseudomonotes tropenbosii* (Dipterocarpaceae) forest in Peña Roja (Middle Caquetá). The litterbag studies were carried out during February 2000 and July 2001 for the plots located in the Caquetá region and between August 2003 and September 2004 in the plots located in the Amazonas. The newly obtained isolates and strains used for comparison are listed in Table 1, together with their origin, substrate information and GenBank accession numbers for ITS, *BenA* and *CaM* genes. Strains of the putative new *Talaromyces* species used in this study were deposited in the culture collection of CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands; the Center for Microbial Biotechnology at the Department of Systems Biology, Technical University of Denmark, Lyngby, Denmark (IBT); and the working collection of the Department of Applied and Industrial Mycology (DTO), housed at CBS-KNAW. The type material of the new taxa is preserved at the herbarium of the University of Antioquia (HUA).

DNA extraction, PCR amplification and sequencing

DNA extractions were made from strains grown for 7–14 days on MEA using the UltraClean® Microbial DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA, USA), and extracted DNA was stored at −20 °C. ITS, *CaM* and *BenA* gene regions were amplified and sequenced using previously described methods (Visagie et al. 2014; Yilmaz et al. 2014).

Phylogeny

Sequence contigs were assembled in SeqMan v. 9.0.4 (DNASTAR, Inc., Madison, WI, USA). The newly generated sequences were included in a data set including sequences obtained from Yilmaz et al. (2014) and supplemented with sequences of new species that were subsequently described (Visagie et al. 2015; Wang et al. 2016; Yilmaz et al. 2016). The dataset for each gene was aligned using the MUSCLE software included in the MEGA v. 6.0.6 software package (Tamura et al. 2013). The aligned ITS, *BenA* and *CaM* data were analyzed using the maximum likelihood (ML) method. The model for ML was selected based on the Akaike information criterion (AIC) calculated in MEGA 6.06. The analysis was performed by calculating an initial tree using BIONJ, and the subsequent heuristic using Nearest-Neighbour-Interchange (NNI). Bootstrap support was calculated using 1000 replicates.

Morphological analysis

Strains were morphologically studied on different media under different growth conditions. Cultures were inoculated onto Czapek yeast extract agar (CYA), CYA supplemented with 5 % NaCl (CYAS), yeast extract sucrose agar (YES), creatine sucrose agar (CREA), dichloran 18 % glycerol agar (DG18), oatmeal agar (OA) and malt extract agar (MEA; Oxoid malt) at three points on 90-mm Petri dishes and incubated for 7 days at 25 °C in darkness. All media were prepared as described by Visagie et al. (2014). Additional MEA and CYA plates were incubated at 30 °C and 37 °C for 7 days in darkness. After incubation, the diameters of the colonies on the various media were measured. The density of sporulation, obverse and reverse colony colours, and the production of soluble pigments were noted. Colony colour codes refer to Kornerup and Wanscher (1967). Colonies were photographed with a Canon EOS 400D camera. Species were characterized microscopically by preparing slides from MEA. Lactic acid was used as mounting fluid, and excess amounts of conidia were washed with ethanol. Specimens were examined using a ZEISS AxioSkop 2 plus microscope, and the Nikon NIS-Elements D software package was used for capturing photographs and taking measurements. Figure plates were prepared in Adobe® Photoshop® CS6.

Extrolites

The strains isolated during this study were analyzed by high-performance liquid chromatography (HPLC) with diode array detection as described by Houbraken et al. (2012). Three agar plugs from the *Talaromyces* isolates grown on CYA, MEA, YES and OA at 25 °C for 7 days were extracted as described by Smedsgaard (1997). The detected metabolites were identified by comparison with standards according to Kildgaard et al. (2014) and Klitgaard et al. (2014).

Table 1 *Talaromyces* strains used in the phylogenetic analysis

Species	CBS number	Other collection numbers	Substrate and origin	GenBank accession numbers		
				ITS	*BenA*	*CaM*
T. aculeatus	289.48^T	CBS 136670 = IMI 040588 = NRRL 2129 = NRRL A-1474 = IBT 14259 = IBT 4185	Textile, USA	KF741995	KF741929	KF741975
T. aculeatus		IBT 23209 = DTO 093-F5	Soil, Araracuara, dept. Amazonas, Colombia	**KX011511**	**KX011491**	NA
T. aculeatus		IBT 23210 = DTO 093-F6	Soil, Araracuara, dept. Amazonas, Colombia	**KX011514**	**KX011492**	NA
T. aculeatus		IBT 23211 = DTO 093-F7	Soil, Araracuara, dept. Amazonas, Colombia	**KX011512**	**KX011493**	NA
T. aculeatus		IBT 23212 = DTO 093-F8	Soil, Araracuara, dept. Amazonas, Colombia	**KX011515**	**KX011494**	NA
T. aculeatus		DTO 276-H2	Leaf litter, mature forest, Amacayacu, dept. Amazonas, Colombia	**KX011513**	**KX011496**	NA
T. amazonensis	140373^T	IBT 23215 = DTO 093-F9	Leaf litter in from 6-month old litterbag in mature forest in Araracuara, dept. Amazonas, Colombia	**KX011509**	**KX011490**	**KX011502**
T. amazonensis		DTO 276-H4	Leaf litter, mature forest, Araracuara, dept. Amazonas, Colombia	**KX011506**	**KX011495**	NA
T. amazonensis		DTO 276-H5	Leaf litter, 42-years old forest, Araracuara, dept. Amazonas, Colombia	**KX011507**	**KX011497**	NA
T. amestolkiae	132696^T	DTO 179-F5	House dust, Cape Town, South Africa	JX315660	JX315623	KF741937
T. angelicus		KACC 46611	Dried root of *Angelica gigas*, Pyeongchang, Republic of Korea	KF183638	KF183640	KF885259
T. apiculatus	312.59^T	ATCC 18315 = FRR 635 = IMI 068239 = IBT 10894 = IBT 14261	Soil, Japan	KF741983	KF741916	KF741950
T. aurantiacus	314.59^T	IMI 099722 = NRRL 3398	Soil, Georgia	JN899380	KF741917	KF741951
T. australis	137102^T	DTO 273-F5 = IBT14256 = FRR 2005	Soil under pasture, Australia	KF741991	KF741922	KF741971
T. bacillisporus	296.48^T	IMI 040045 = NRRL 1025	Leaf, New York, USA	KM066182	AY753368	KJ885262
T. calidicanius	112002^T	DTO 038-B8	Soil, Taiwan	JN899319	HQ156944	KF741934
T. cnidii		KACC 46617^T	Dried roots of *Cnidium officinale*, Chungbuk, Republic of Korea	KF183639	KF183641	KJ885266
T. columbiensis	113151^T	IBT 23206 = DTO 058-F3	Fresh leaf litter in mature forest in Amacayacu National Park, Dept. Amazonas, Colombia	**KX011503**	**KX011488**	**KX011499**
T. derxii	412.89^T	NHL 2981	Soil, Kurashiki, Japan	JN899327	JX494305	KF741959
T. duclauxii	322.48^T	IMI 040044 = MUCL 28672 = MUCL 29094 = MUCL 29212 = NRRL 1030	Canvas, France	JN899342	JX091384	KF741955
T. emodensis	100536^T	IBT 14990	Soil, Kathmandu, Nepal	JN899337	KJ865724	KJ885269
T. euchlorocarpius		PF 1203^T = DTO 176-I3	Soil, Yokohama, Japan	AB176617	KJ865733	KJ885271
T. flavovirens	102801^T	IBT 27044	*Quercus suber* leaf litter, Catalonia, Spain	JN899392	JX091376	KF741933
T. flavus	310.38^T	IMI 197477 = NRRL 2098	Unknown source, New Zealand	JN899360	JX494302	KF741949
T. francoae	113134^T	IBT 23221 = DTO 056-D9	Leaf litter from 4-month old litterbag in *Pseudomonotes tropenbosii* (Dipterocarpaceae) forest in Peña Roja, Dept. Amazonas, Colombia	**KX011510**	**KX011489**	**KX011501**
T. funiculosus	272.86^T	IMI 193019	*Lagenaria vulgaris*, India	JN899377	JX091383	KF741945
T. fuscoviridis	193.69^T	IBT 14846 = IBT 32646	Soil, the Netherlands	KF741979	KF741912	KF741942
T. galapagensis	751.74^T	IFO 31796	Soil beneath *Maytenus obovata*, Galapagos Island, Ecuador	JN899358	JX091388	KF741966
T. hachijoensis		IFM 53624^T = PF 1174	Soil, Hachijō-jima, Japan	AB176620	NA	NA
T. liani	225.66^T	IMI 098480 = NRRL 3380 = VKM F-301	Soil, China	JN899395	JX091380	KJ885257

Table 1 (continued)

Species	CBS number	Other collection numbers	Substrate and origin	GenBank accession numbers		
				ITS	*BenA*	*CaM*
T. intermedius	152.65^T	IMI 100874	Alluvial pasture and swamp soil, Nottingham, England	JN899332	JX091387	KF741941
T. kendrickii	136666^T	DTO 273-F4 = IBT 13593	Forest soil, Canada	KF741987	KF741921	KF741967
T. kendrickii	136669	DTO 273-F8 = IBT 14128	Soil from damping-off box, Nigeria	KF741988	KF741925	KF741968
T. macrosporus	317.63^T	FRR 404 = IMI 197478	Apple juice, Stellenbosch, South Africa	JN899333	JX091382	KF741952
T. macrosporus	116297	IBT 23205 = DTO 056-D8 = DTO 189-B9	Decomposing leaves after 4 months; Middle Caquetá, Araracuara, Colombia	**KX011505**	**KX011486**	NA
T. marneffei	388.87^T	CBS 334.59 = IMI 068794ii = IMI 068794iii	Bamboo rat (*Rhizomys sinensis*), Vietnam	JN899344	JX091389	KF741958
T. mimosinus	659.80^T	FRR 1875 = IMI 223991	Soil from creek bank, New South Wales	JN899338	KJ865726	KJ885272
T. muroii	756.96^T	PF 1153	Soil, Chingpu, Taiwan	JN899351	KJ865727	KJ885274
T. oumae-annae	138208^T	DTO 269-E8	House dust, Cape Town, South Africa	KJ775720	KJ775213	KJ775425
T. purgamentorum	113145^T	IBT 23220 = DTO 056-E1	Leaf litter from 4-month old litterbag in *Pseudomonotes tropenbosii* (Dipterocarpaceae) forest in Peña Roja, Dept. Amazonas, Colombia	**KX011504**	**KX011487**	**KX011500**
T. purpurogenus	286.36^T	IMI 091926	Parasitic on a culture of *Aspergillus oryzae*, Japan	JN899372	JX315639	KF741947
T. panamensis	128.89^T	IMI 297546	Soil, Barro Colorado Island, Panama	JN899362	HQ149327	KF741936
T. paucisporus		PF 1150^T = IFM 53616	Soil, Aso-machi, Japan	AB176603	NA	NA
T. pinophilus	631.66^T	CECT 2809 = IMI 114933	PVC, France	JN899382	JX091381	KF741964
T. primulinus	321.48^T	FRR 1074 = IMI 040031 = MUCL 31321 = MUCL 31330 = NRRL 1074	Unknown source, USA	JN899317	JX494305	KF741954
T. proteolyticus	303.67^T	NRRL 3378	Granite soil, Ukraine	JN899387	KJ865729	KJ885276
T. ruber	132704^T	DTO 193-H6 = IBT 10703	Aircraft fuel tank, UK	JX315662	JX315629	KF741938
T. rubicundus	342.59^T	IMI 099723 = NRRL 3400	Soil, Georgia	JN899384	JX494309	KF741956
T. sayulitensis	138204^T	DTO 245-H1	House dust, Sayulita, Mexico	KJ775713	KJ775206	KJ775422
T. siamensis	475.88^T	IMI 323204	Forest soil, Lampang, Thurn District, Ban Daen Tham, Thailand	JN899385	JX091379	KF741960
T. stellenboschiensis	135665^T	DTO 181-A2 = DAOM 241021 = IBT 32631	Soil, Stellenbosch, South Africa	JX091471	JX091605	JX140683
T. stipitatus	375.48^T	IMI 039805 = NRRL 1006	Decaying wood, Louisiana, USA	JN899348	KM111288	KF741957
T. stollii	408.93^T	DTO 060-E4	AIDS patient, the Netherlands	JX315674	JX315633	JX315646
T. thailandensis	133147^T	KUFC 3399	Soil, Thailand	JX898041	JX494294	KF741940
T. unicus	100535^T	CCRC 32703 = IBT 18385 = FRR 4436	Soil, Taiwan	JN899336	KJ865735	KJ885283
T. veerkampii	500.78^T	DTO 258-I8 = IBT 14845 = IBT 32648	Soil, Dep. de Meta, Municipio de Villavicencio, Colombia	KF741984	KF741918	KF741961
T. verruculosus	388.48^T	CBS 136671 = IMI 040039 = NRRL 1050 = FRR 1050 = IBT 10891 = IBT 32644	Soil, Texas, USA	KF741994	KF741928	KF741974
T. viridis	114.72^T	NRRL 5575	Soil, Australia	AF285782	JX494310	KF741935
T. viridulus	252.87^T	FRR 1863 = IMI 288716	Soil, New South Wales, Australia	JN899314	JX091385	KF741943

Newly generated sequences are marked in bold

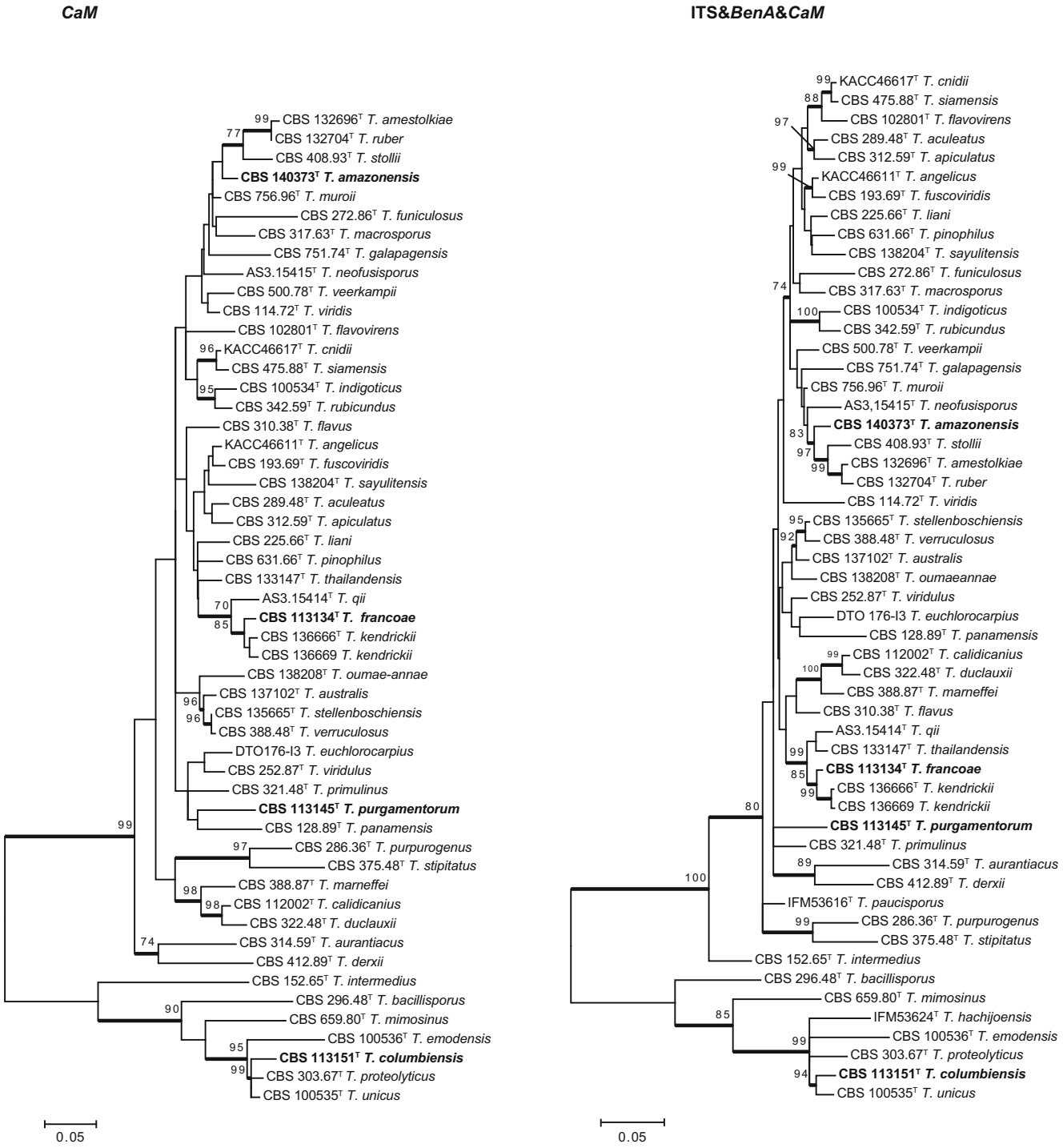

Fig. 1 Phylogenies based on the ITS, *BenA, CaM* and combined data set showing the relationship between the new species described in the study and other members of *Talaromyces* sections *Talaromyces* and *Bacillispori*. Strains of known species (*T. aculeatus* and *T. macrosporus*) isolated in the course of this study are marked with *asterisks* in ITS and *BenA* phylograms. Strains belonging to new species are indicated by *bold text*. Support in nodes are indicated by *thickened branches* for bootstrap values ≥ 70, % and ^{T} indicates ex-type strains

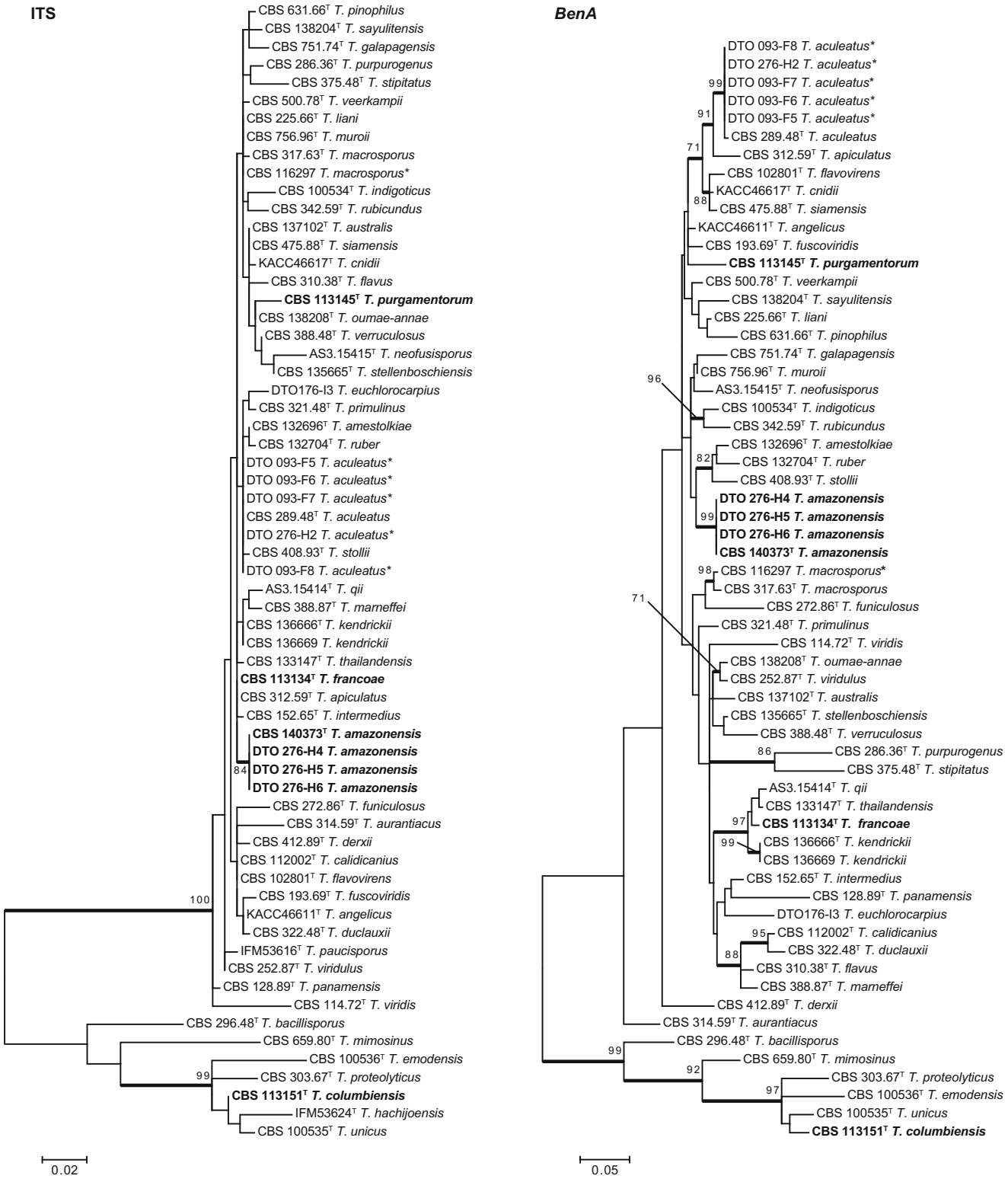

Fig. 1 continued.

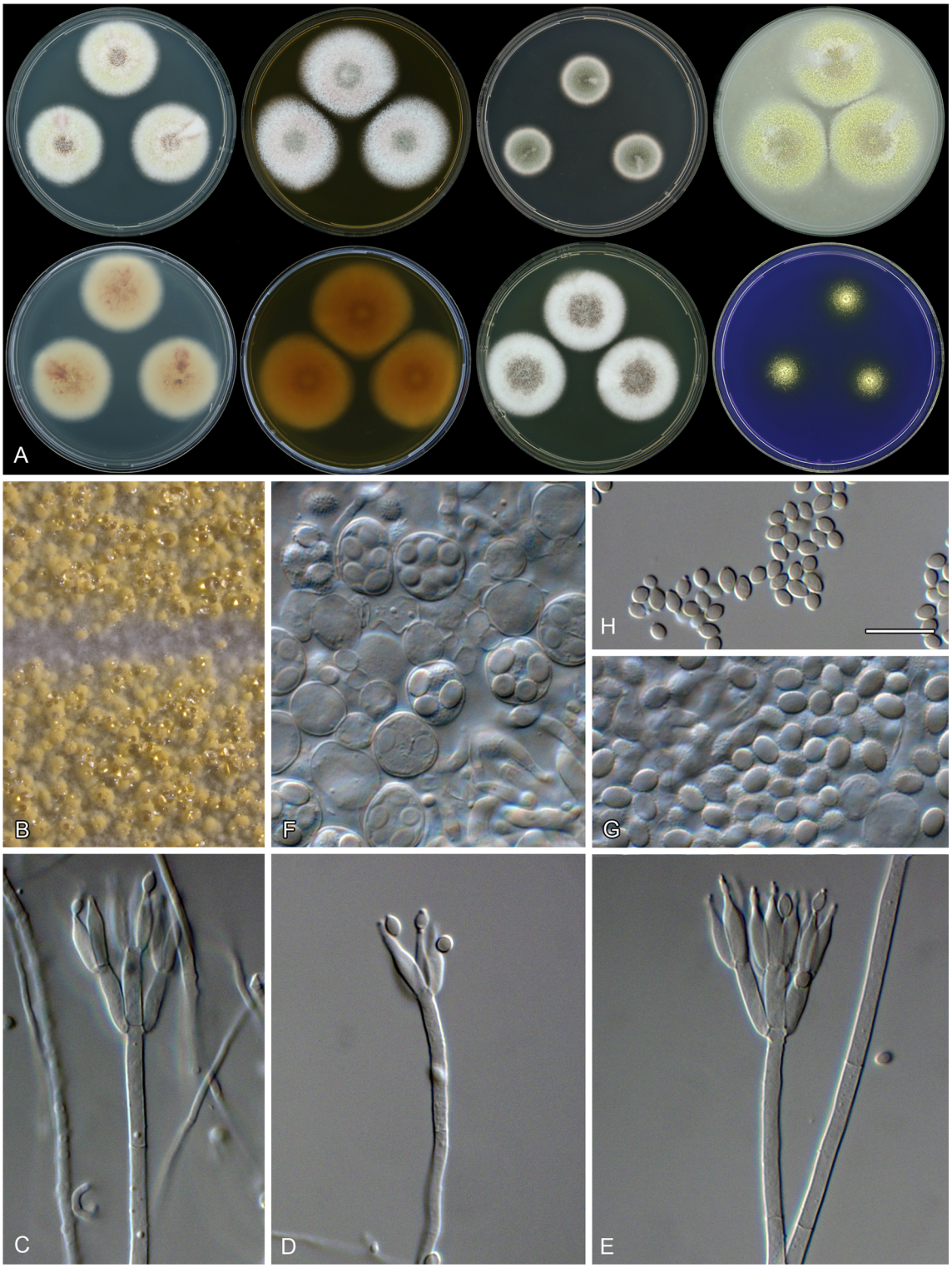

Fig. 2 Morphological characters of *Talaromyces amazonensis* (CBS 140373^{T}). **a** Colonies from left to right (*top row*) CYA, MEA, DG18 and OA; (*bottom row*) CYA reverse, MEA reverse, YES and CREA. **b** Colony texture and ascomata on OA after 2-week incubation. **c**–**e** Conidiophores. **f** Asci and ascospores. **g** Ascospores. **h** Conidia. *Scale bar*: **h** = 10 μm applies to **c**–**h**

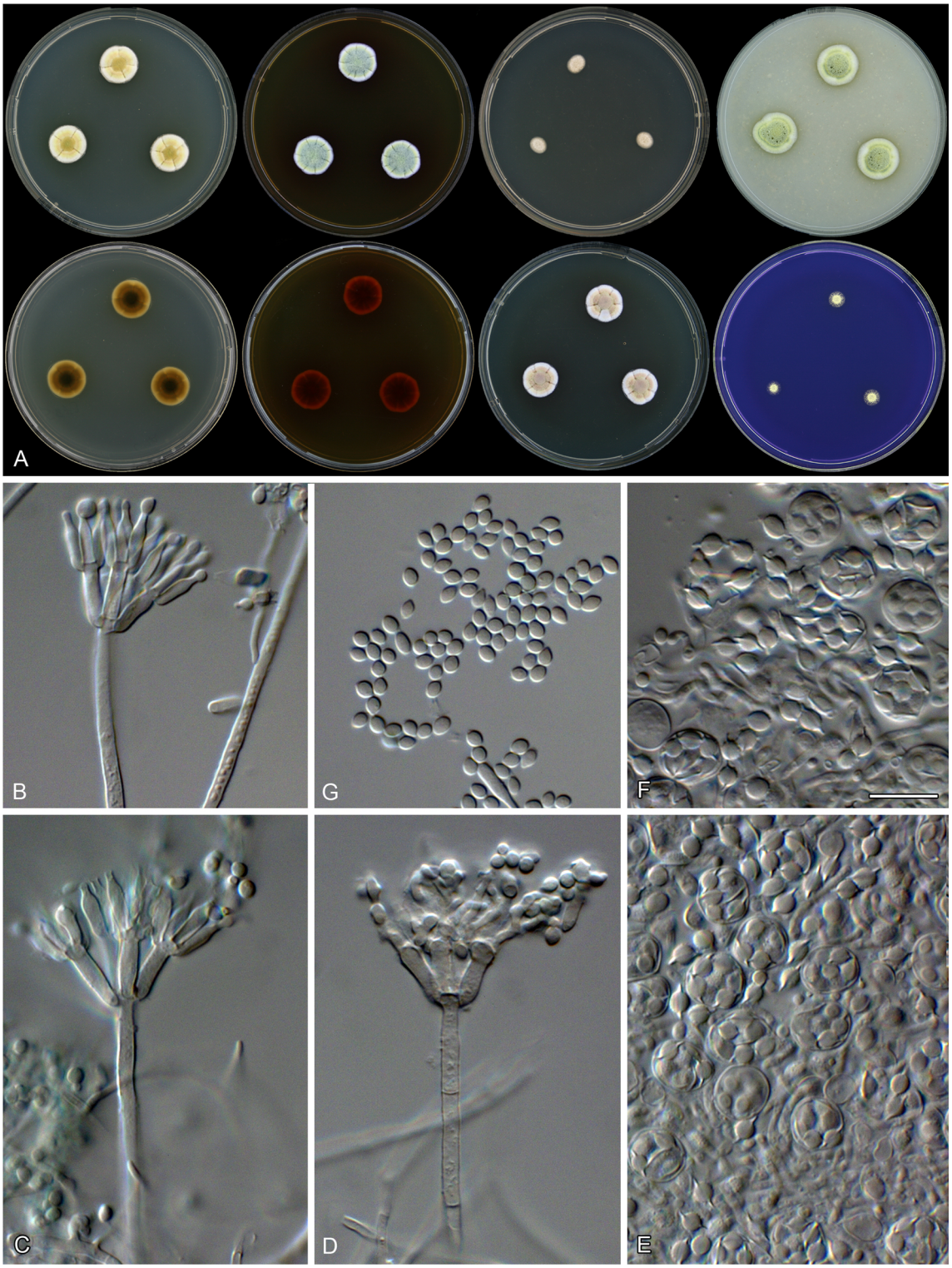

Fig. 3 Morphological characters of *Talaromyces columbiensis*, CBS 113151[T]. **a** Colonies from left to right (*top row*) CYA, MEA, DG18 and OA; (*bottom row*) CYA reverse, MEA reverse, YES and CREA. **b**–**d** Conidiophores. **e**, **f** Asci and ascospores. **g** Conidia. *Scale bar*: **f** = 10 μm applies to **b**–**g**

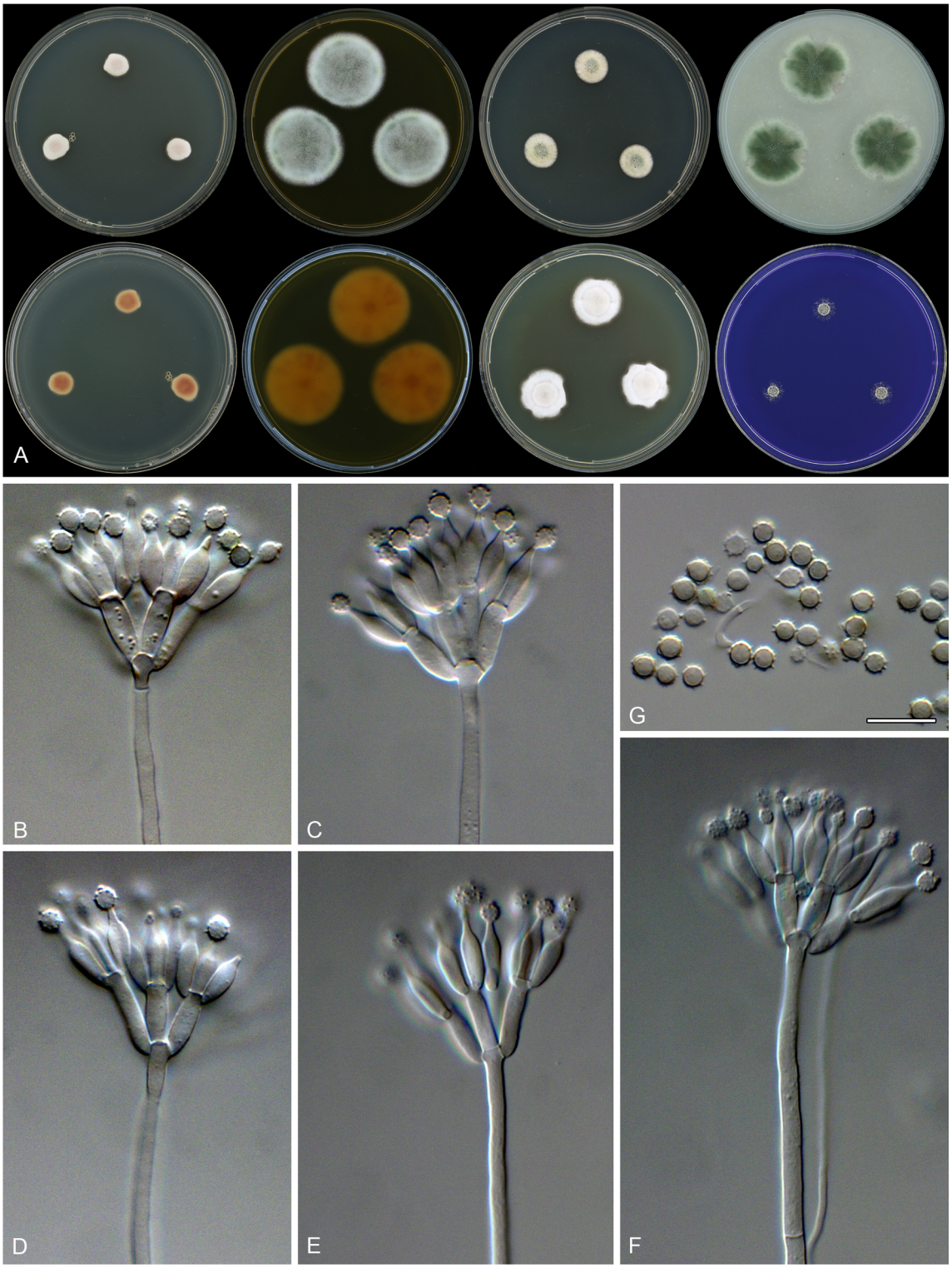

Fig. 4 Morphological characters of *Talaromyces francoae*, CBS 113134[T]. **a** Colonies from left to right (*top row*) CYA, MEA, DG18 and OA; (*bottom row*) CYA reverse, MEA reverse, YES and CREA. **b**–**f** Conidiophores. **g** Conidia. *Scale bar*: **g** = 10 μm applies to **b**–**g**

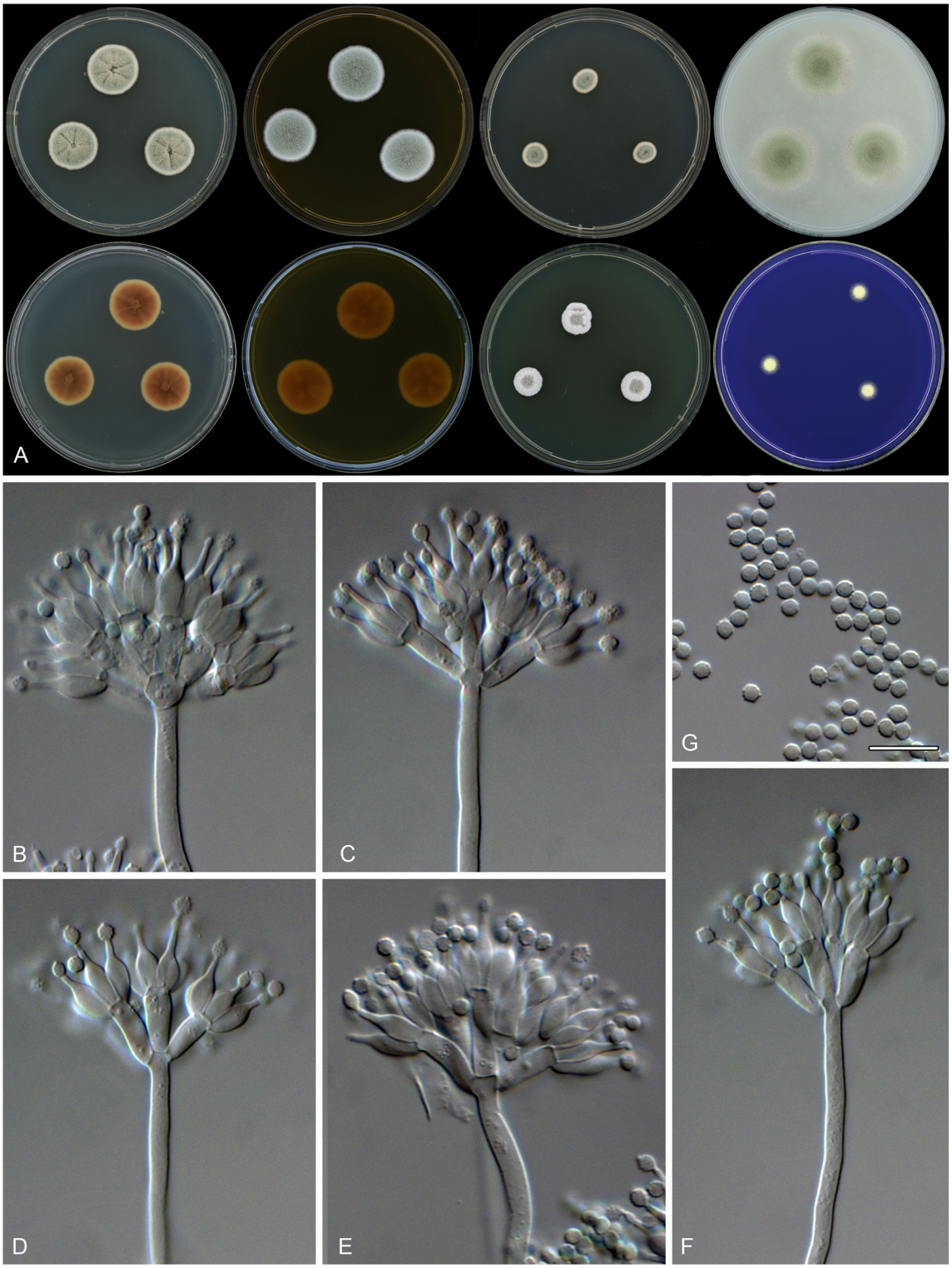

Fig. 5 Morphological characters of *Talaromyces purgamentorum*, CBS 113145[T]. **a** Colonies from left to right (*top row*) CYA, MEA, DG18 and OA; (*bottom row*) CYA reverse, MEA reverse, YES and CREA. **b**–**f** Conidiophores. **g** Conidia. *Scale bar*: **g** = 10 μm applies to **b**–**g**

Results

Diversity of *Talaromyces* species

ITS barcoding of the isolated fungi revealed the presence of various *Talaromyces* species among the other fungi isolated from the litterbags. Two known species, *T. aculeatus* and *T. macrosporus*, were isolated from the samples, and several other isolates seemed to represent species unknown to science. They are further studied in detail below and described as new species *Talaromyces amazonensis*, *T. columbiensis*, *T. francoae* and *T. purgamentorum*.

Phylogeny

The phylogenies presented in Fig. 1 show that the isolates studied here are accommodated in *Talaromyces* section *Talaromyces* (i.e., *T. amazonensis*, *T. francoae* and *T. purgamentorum*) and section *Bacillispori* (*T. columbiensis*). The concatenated data set was 1348 bp in length (ITS 458 bp; *BenA* and *CaM* 445 bp). The Tamura 3-parameter (T92) with gamma distribution (+G) and invariant sites (+I) was found to be the most suitable model for the ML analysis of the combined tree (Fig. 1). For the single gene trees, the T92+G+I model was found to be the most suitable for the ML analysis of the ITS alignment, while the Kimura 2-parameter (K2)+G+I was the most suitable model for both *BenA* and *CaM* data sets. ML trees were used to present the phylogenetic data, with bootstrap values (bs) shown near the nodes of the phylogram (Fig. 1). The *BenA* and *CaM* data sets had sufficient discriminatory power to differentiate the new species from other recognized species. The ITS barcode of *T. francoae* (CBS 113134^T) was identical to that of *T. apiculatus* (CBS 312.59^T).

Talaromyces columbiensis (CBS 113151^T) is located close to *T. unicus*, and *T. francoae* (CBS 113134^T) is closely related to *T. kendrickii* in all phylogenies. Both *T. amazonensis* (CBS 140373^T) and *T. purgamentorum* (CBS 113145^T) shift their positions between phylogenies, making it difficult to determine their closest relatives.

Morphology

The new taxa share similarities with other known species, but can also be differentiated by various characters. Detailed descriptions of the new species are given in the Taxonomy section, and the differences from the other *Talaromyces* species are summarized in the Discussion. In short, *T. amazonensis* (CBS 140373^T) produced yellow ascomata on OA at 25 and 30 °C after 1–2 weeks of incubation (Fig. 2), and its ascospores resembled those of *T. flavus, T. muroii*, *T. liani* and *T. thailandensis. Talaromyces columbiensis* (CBS 113151^T) produced yellow ascomata on MEA, smooth ascospores with a single equatorial ridge, and has no growth at 37 °C (Fig. 3). No sexual state was observed in *T. francoae* (CBS 113134^T) or *T. purgamentorum* (CBS 113145^T). Both species produced ampulliform phialides with a tapering neck and spiny, globose conidia (Figs. 4 and 5). They were not able to grow at 37 °C and lacked acid production on CREA. *Talaromyces*

Table 2 Production of extrolites by the *Talaromyces* species isolated in this study

Species	Culture collection numbers	Extrolites
T. aculeatus	IBT 23209 = DTO 093-F5	Altenusin, alternariol, an apolar dibenzofuran, mitorubrinic acid, penicillide, purpactin A, talaroderxines
T. aculeatus	IBT 23210 = DTO 093-F6	Alternariol, mitorubrinic acid, purpactin A, vermicillin
T. aculeatus	IBT 23211 = DTO 097-F7	Alternariol, mitorubrinic acid, purpactin A, vermicillin
T. aculeatus	IBT 23212 = DTO 093-F8	Alternariol, mitorubrinic acid, purpactin A, vermicillin
T. amazonensis	CBS 140373^T = IBT 23215 = DTO 093-F9	berkelic acid, duclauxin, mitorubrinic acid, vermicillin
T. amazonensis	IBT 23216 = DTO 276-H5	Berkelic acid, duclauxin, mitorubrinic acid
T. columbiensis	CBS 113151^T = IBT 23206 = DTO 053-F3	A corymbiferan lactone, duclauxin, mitorubrin, mitorubrinic acid, wortmannin
T. francoae	CBS 113134^T = IBT 23221 = DTO 056-D9	Berkelic acid, mitorubrin, mitorubrinic acid, vermicillin
T. macrosporus	CBS 116297 = IBT 23205 = DTO 189-B9	A corymbiferan lactone, duclauxin
T. purgamentorum	CBS 113145^T = IBT 23220 = DTO 056-E1	A dibenzofuran, penicillide, purpactin A, a shamixanthone, a violaceol

purgamentorum exhibited restricted growth on DG18 and YES compared to *T. francoae*.

Extrolites

The species described here produce various extrolites, all of which are previously found in *Talaromyces* (Frisvad et al. 1990). Especially common are mitorubrinic acid, alternariol and the penicillides (Table 2). Details on the extrolites found in each species are given in the species descriptions.

Discussion

This study focused on four novel *Talaromyces* species isolated from leaf litter in several Colombian lowland rain forests. The multiple gene phylogenies (ITS, *BenA* and *CaM*) resolved strains into four distinct lineages that represent species. Based on a multigene phylogeny (ITS, *BenA* and *RPB2*), Yilmaz et al. (2014) divided the genus into seven clades and provided a sectional classification. Three of the species from this study are located in *Talaromyces* section *Talaromyces*, whereas one species (*T. columbiensis*) falls in section *Bacillispori*. Previous studies showed that ITS, which is the accepted DNA barcode for fungi (Schoch et al. 2012), is not sufficient to distinguish all *Talaromyces* species (Yilmaz et al. 2012; Frisvad et al. 2013; Manoch et al. 2013; Yilmaz et al. 2014). As a result, Yilmaz et al. (2014) proposed the use of *BenA* as a suitable secondary barcode marker for identification of *Talaromyces* isolates. With the exception of *T. francoae*, however, all newly described species could be identified by using ITS alone. *BenA* and *CaM* data sets showed that all novel species are clearly distinct from previously described *Talaromyces* species.

Visagie et al. (2015) revised *Talaromyces* species producing ampulliform phialides and rough-walled, globose conidia, and recognized eight species. Except for *T. kendrickii*, all species could grow at 37 °C. In this study, *T. francoae* and *T. purgamentorum* have ampulliform phialides and rough-walled, globose conidia. Neither species grows at 37 °C, and neither produces acid on CREA. These two characters of the new species are shared with *T. kendrickii*. However, on CYA at 25 °C, *T. kendrickii* (25–31 mm) grows faster than *T. francoae* (8–10 mm) and *T. purgamentorum* (19–20 mm). *Talaromyces francoae* differs from *T. purgamentorum* by their growth rates on CYA and YES. The former species exhibits restricted growth on CYA (8–10 mm) and moderately fast growth on YES (20–22 mm), while *T. purgamentorum* attains a diameter on CYA of 19–20 mm and 10–12 mm on YES. *Talaromyces amazonensis* produces yellow ascomata with spiny, ellipsoidal ascospores, and these characters are common in the genus *Talaromyces*. Ascospores of *T. amazonensis* resemble those of *T. flavus, T. muroii, T. thailandensis*, and *T. liani*. Both *T. flavus* and *T. muroii* grow more restrictedly on CYA than *T. amazonensis* (9–16 mm vs. 30–38 mm). *Talaromyces amazonensis* differs from *T. thailandensis* by its ability to grow at 37 °C. The main difference between *T. liani* and *T. amazonensis* is the ascoma colour. *Talaromyces liani* has orange-red ascomata, whereas the ascomata of *T. amazonensis* are yellow. *Talaromyces columbiensis* produces abundant yellow ascomata and smooth-walled ascospores with a single ridge on MEA after 2 weeks of incubation at 25 °C. This species is phylogenetically closely related to *T. unicus*, which also produces ascospores with a single equatorial ridge. However, *T. unicus* differs by the production of ascospores with a very rough to spiny wall. *Talaromyces stipitatus* also produces ellipsoidal, smooth-walled ascospores with a single equatorial ridge. However, this species grows faster on standard agar media (CYA, MEA, OA and YES) and is able to grow on CYA incubated at 37 °C.

Talaromyces is an important genus in biotechnology and in medical and food mycology (Yilmaz et al. 2014). *Talaromyces* species are isolated worldwide from many kinds of substrates, including house dust, decaying leaves, soil, air, compost, food products, humans and animals. The fungi are considered key players in leaf litter decomposition because of their ability to produce a wide range of extracellular enzymes (de Boer et al. 2005), and some *Talaromyces* species also produce cellulose-degrading enzymes (Pol et al. 2012; Maeda et al. 2013; Fuji et al. 2014). In this study, we isolated six *Talaromyces* species from leaf litter in the Colombian Amazon region. Two of them, *T. aculeatus* and *T. macrosporus*, have been previously described. The other four species are new to the literature, and thus far found only in decomposed leaf litter in Amazonia, Colombia.

The new *Talaromyces* species were efficient producers of a series of anticancer compounds. *Talaromyces amazonensis* in particular produced three different anticancer compounds: duclauxin, berkelic acid and vermicillin. It would be interesting to determine whether these anticancer compounds have a synergistic effect when combined. Another interesting compound found in *T. columbiensis* was wortmannin, also an anticancer compound, with several additional biological activities.

Taxonomy

Talaromyces amazonensis Yilmaz, López-Quintero, Vasco-Pal., Frisvad & Houbraken, **sp. nov.** Mycobank MB816230. Fig. 2.

Etymology: From Amazonas, the department from which the species was isolated.

Diagnosis: Moderately fast growth on CYA, MEA, YES and OA at 25 °C, restricted growth on DG18 at 25 °C, moderate acid production on CREA. Abundant yellow ascomata produced on MEA and OA after 1–2 weeks at 25 °C with broadly ellipsoidal, thick-walled, spiny ascospores.

Typus: **Colombia**, dept. Amazonas, Araracuara community in the Middle Caquetá, ex mixed leaves in litterbag, after 6 months of decomposition in a mature forest, isolated in July 2000, *C. López-Quintero* (holotype HUA 197223; culture ex-type CBS 140373 = IBT 23215 = DTO 093-F9).

ITS barcode: KX011509 (alternative markers: *BenA* = KX011490; *CaM* = KX011502).

Colony diameter 7 days (mm): CYA 30–38; CYA 30 °C 35–42; CYA 37 °C 19–22; MEA 40–45; MEA 30 °C 50–55; DG18 20–25; CYAS No growth; OA 30–45; CREA 12–18; YES 35–42.

Colony characters: CYA 25 °C, 7 days: Colonies slightly raised at centre, slightly sulcate; margins low, plane, entire (2 mm); mycelium white and in the centre brownish red due to the pigmentation in reverse; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse light yellow (4A4) with dark red (10C8) dots. MEA 25 °C, 7 days: Colonies slightly raised at centre, plane; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation sparse to moderately dense at centre, conidia *en masse* dull green (27D3); soluble pigments absent; exudates absent; reverse greyish orange (5B6–6B6). YES 25 °C, 7 days: Colonies sunken at centre, slightly sulcate; margins low, plane, entire (2–3 mm); mycelium white, in some parts pastel-red and in the centre yellowish brown (5E4) due to the reverse pigment; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse light yellow (4A4) with dark red (10C8) dots. DG18 25 °C, 7 days: Colonies low, plane; margins low, plane, entire (1–2 mm); mycelium white; texture velvety; sporulation dense, conidia *en masse* dull green (25D5–26D4); soluble pigments absent; exudates absent; reverse greenish white to greenish grey (28A2–28B2). OA 25 °C, 7 days: Colonies low, plane, yellow ascomata also at 30 °C abundant; margins low, plane, entire (4–5 mm); mycelium yellow; texture floccose; sporulation absent; soluble pigments absent; exudates absent; reverse pastel-yellow. CREA 25 °C, 7 days: weak growth, moderate acid production.

Micromorphology: Conidiophores biverticillate, sometimes monoverticillate; stipes smooth-walled, 30–220 × 2–3 μm; metulae divergent, two to five, 7.5–12 × 2.4–3.8 μm; phialides acerose, two to five per metula, 8–13 × 2–3 μm; conidia smooth-walled, ellipsoidal, 2.5–4(–6) × 2–3 μm. Ascomata bright yellow, globose to subglobose, abundantly ripening within 1–2 weeks on OA at 25 °C, covered with a few layers of well-developed networks of yellow hyphae; asci broadly globose to subglobose, 9–13 × 8–12 μm; ascospores broadly ellipsoidal, thick-walled, spiny, 3–5.5 × 2–4 μm.

Extrolites: *Talaromyces amazonensis* produces berkelic acid, duclauxin, mitorubrinic acid and vermicillin. Berkelic acid was first found as an anticancer agent in *T. ruber* (Stierle et al. 2006). The anticancer agent duclauxin was first found in *T. duclauxii*, but this compound has also been reported from *T. macrosporus* (Shibata et al. 1965; Frisvad et al. 1990; Bryant et al. 1993). Duclauxin was also reported from *Penicillium herquei* and *P. manginii* (Bryant et al. 1993; Cao et al. 2015), but the strains used had been misidentified, and the producers were *Talaromyces* species as well. Vermicillin is the third anticancer agent from *T. amazonensis* (Fuska et al. 1979). Mitorubrinic acid is a common azaphilone metabolite in the genus *Talaromyces* (Frisvad et al. 1990).

Talaromyces columbiensis Yilmaz, López-Quintero, Vasco-Pal., Frisvad & Houbraken, **sp. nov.** Mycobank MB 816231. Fig. 3.

Etymology: From Colombia, the country where the species was isolated.

Diagnosis: Restricted growth on CYA, MEA, YES, OA and DG18 at 25 °C and no growth at 37 °C. Yellow ascomata abundant on MEA after 2 weeks at 25 °C with ellipsoidal, smooth, single equatorial ridge ascospores.

Typus: **Colombia**, Amazonia, Natural Park Amacayacu, ex litterbag containing fresh mixed leaves from mature forest, isolated in September 2004, *C. López-Quintero* (holotype HUA 197225; cultures ex-type CBS 113151 = IBT 23206 = DTO 058-F3).

ITS barcode: KX011503 (alternative markers: *BenA* = KX011488; *CaM* = KX011499).

Colony diameter 7 days (mm): CYA 15–17; CYA 30 °C 18; CYA 37 °C No growth; MEA 15–17; MEA 30 °C 16–17; DG18 5; CYAS 3; OA 15–17; CREA 8–10; YES 14–15.

Colony characters: CYA 25 °C, 7 days: Colonies low, sulcate; margins low, plane, entire (1 mm); mycelium white and yellow; texture floccose; sporulation sparse; soluble pigments absent; exudates absent; reverse yellowish brown (5F5) centre fading to brownish orange to yellowish brown (5C5–5D5–5E5). MEA 25 °C, 7 days: Colonies raised at centre, sulcate; margins low, plane, entire (1 mm); mycelium dominantly yellow, in the margins white; texture floccose; sporulation sparse, conidia *en masse* greyish green (28C5–28D5); soluble pigments pale red; exudates absent; reverse brown (7E6) fading to reddish orange (7B7). YES 25 °C, 7 days: Colonies raised at centre, sulcate; margins low, plane, entire (1 mm); mycelium white, brownish orange to light brown (7C5–7D5); texture floccose; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse brownish orange (5C5) centre fading to greyish orange (5B5). DG18 25 °C, 7 days: Colonies covered with sterile white mycelium; reverse yellowish white (4A2). OA 25 °C, 7 days: Colonies raised at centre, slightly

sulcate; margins low, plane, entire (1–2 mm), no transparent zone; mycelium white and yellow; texture loosely funiculose to velvety; sporulation moderately dense at centre, conidia *en masse* dull green (26D4); soluble pigments absent; exudates small, clear droplets; reverse pastel orange-yellow. CREA 25 °C, 7 days: Weak growth, weak acid production.

Micromorphology: Conidiophores biverticillate; stipes smooth-walled, (40–) 50–130 (–145) × 2.4–3 μm; metulae divergent, three to six, 8.5–11.5 × 2.4–3.5 μm; phialides acerose, sometimes atypical, two to six per metula, 7–9.5 × 1.5–2.5 μm; conidia smooth-walled, ovoid to ellipsoidal, 2.5–3 × (1.8–) 2–2.5 μm. Ascomata bright yellow, globose to subglobose, ripening within 1–2 weeks on OA at 25 °C, covered with layers of well-developed networks of yellow hyphae; asci broadly globose to subglobose, 7–9 × 7.5–10 μm; ascospores ellipsoidal, finely rough to spiny, usually with a single equatorial ridge, 2.5–4.2 (–5) × 2.5–3.5 μm.

Extrolites: *Talaromyces columbiensis* produced duclauxin and several related naphthalenones, but also mitorubrins and wortmannin. Wortmannin was originally discovered as an antifungal agent, but it is also a potent enzyme inhibitor of regulatory kinases and is thus an interesting anticancer drug candidate (Wipf and Halter 2005). Wortmannin was originally reported from *T. wortmannii* and *T. flavus* (Brian et al. 1957), but these two species are not able to produce wortmannin (Yilmaz et al. 2014). It is thus interesting that *T. columbiensis* can produce this compound. Wortmannin has also been mentioned as a hemorrhagic mycotoxin (Abbas and Mirocha 1998) and an inhibitor of aflatoxin biosynthesis (Lee et al. 2007).

Talaromyces francoae Yilmaz, López-Q., Vasco-Pal. & Houbraken, **sp. nov.** Mycobank MB 816232. Fig. 4.

Etymology: named after Franco, the family name of Dr. Ana Esperanza Franco-Molano, who made major contributions to Colombian mycology.

Diagnosis: Conidiophores biverticillate with ampulliform phialides that taper to a very thin neck producing rough-walled, verrucose conidia. Lack of acid production on CREA and absence of growth on CYA at 37 °C. Restricted growth on CYA at 25 °C (8–10 mm).

Typus: **Colombia**, Dept. Amazonas, Peña Roja, ex leaf litter from 4-month old litterbag in *Pseudomonotes tropenbosii* (*Dipterocarpaceae*) forest, isolated in March 2000, *C. López-Quintero* (holotype HUA 197224; culture ex-type CBS 113134 = IBT 23221 = DTO 056-D9).

ITS barcode: KX011510 (alternative markers: *BenA* = KX011489; *CaM* = KX011501).

Colony diameter 7 days (mm): CYA 8–10; CYA 30 °C 29–30; CYA 37 °C No growth; MEA 20–21; MEA 30 °C 37–38; DG18 10–11; CYAS No growth; OA 35–37; CREA 5–9; YES 20–22.

Colony characters: CYA 25 °C, 7 days: Colonies raised at centre, slightly sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation moderately dense, conidia *en masse* dull to greyish green (25D4–25D5); soluble pigments absent; exudates absent; reverse pale orange (5A3–6A3). MEA 25 °C, 7 days: Colonies raised, slightly sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose and velvety; sporulation dense, conidia *en masse* dull to greyish green (26D4–27D4); soluble pigments absent; exudates absent; reverse greyish orange (5B6) with reddish brown (8D8) dots and circle. YES 25 °C, 7 days: Colonies raised at centre, sulcate; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse brownish red (8C8) centre fading to light orange (5A4). DG18 25 °C, 7 days: Colonies sterile, raised, plane; margins low, plane, entire (2 mm); mycelium white; texture floccose; sporulation absent to sparse; soluble pigments absent; exudates clear droplets; reverse light orange (5A4). OA 25 °C, 7 days: Colonies low, plane; margins low, plane, entire (3–4 mm); mycelium white; texture velvety; sporulation moderately dense to dense, conidia *en masse* greyish green (26D5–26E5); soluble pigments absent; exudates absent; reverse pastel-red in centre fading to beige (at 30 °C violet red). CREA 25 °C, 7 days: weak growth, acid production absent.

Micromorphology: Conidiophores biverticillate; stipes smooth-walled, 125–450 × 2.2–3 μm; metulae divergent, 3–6, 8–13 × 2.5–4.5 μm; phialides ampulliform, tapering to a very thin neck, 3–6 per metula, 8.5–12 × 2.5–4 μm; conidia verrucose, rough-walled, globose, 2.5–4 × 2.5–4 μm.

Extrolites: Talaromyces francoae produces berkelic acid, mitorubrin, mitorubrinic acid and vermicillin.

Talaromyces purgamentorum Yilmaz, López-Quintero, Vasco-Pal. & Houbraken, **sp. nov.** Mycobank MB 816233. Fig. 5.

Etymology: named after de original substrate of the type strain, decomposed leaf litter debris.

Diagnosis: Conidiophores biverticillate with ampulliform phialides that taper to a very thin neck producing rough-walled, verrucose conidia. Lack of acid production on CREA and absence of growth on CYA at 37 °C. Restricted growth on YES (10–12 mm) and DG18 (5–6 mm) at 25 °C.

Typus: **Colombia**, dept. Amazonas, Peña Roja, ex mixed leaf litter from 4 months old litterbag in *Pseudomonotes tropenbosii* (*Dipterocarpaceae*) forest, isolated in March 2000, *C. López-Quintero* (holotype HUA 197222; culture ex-type CBS 113145 = IBT 23220 = DTO 056-E1).

ITS barcode: KX011504 (alternative markers: *BenA* = KX011487; *CaM* = KX011500).

Colony diameter, 7 days (mm): CYA 19–20; CYA 30 °C 24–25; CYA 37 °C No growth; MEA 20–22; MEA 30 °C 25–28; DG18 5–6; CYAS 2–3; OA 33–35; CREA 7–10; YES 10–12.

Colony characters: CYA 25 °C, 7 days: Colonies raised at centre, sunken at centre, sulcate; margins low, plane, entire (1 mm); mycelium white; texture loosely funiculose and

velvety; sporulation dense, conidia *en masse* dull green (26D4–26E4); soluble pigments absent; exudates absent; reverse brown (6E7) centre reddish brown fading to greyish yellow (8D6 and 4B5). MEA 25 °C, 7 days: Colonies low, slightly sulcate; margins low, plane, entire (1–2 mm); mycelium white; texture velvety; sporulation dense, conidia *en masse* dull green (26D4–26E4); soluble pigments absent; exudates absent; reverse brownish orange (5C6–6C6). YES 25 °C, 7 days: Colonies slightly raised, sterile white aerial mycelium, slightly sulcate; margins low, plane, entire (<1 mm); mycelium white; texture floccose and funiculose; sporulation absent to sparse; soluble pigments absent; exudates absent; reverse bronze brown (5E5) centre fading to greyish orange (5B5). DG18 25 °C, 7 days: Colonies slightly raised, plane; margins low, plane, entire (<1 mm); mycelium white; texture velvety; sporulation dense, conidia *en masse* dull green (26D4–26E4); soluble pigments absent; exudates absent; reverse light brown (5D4–5D5). OA 25 °C, 7 days: Colonies low, plane; margins low, plane, entire (4–5 mm); mycelium white; texture velvety; sporulation moderately dense, conidia *en masse* dull green (28D4); soluble pigments absent; exudates absent; reverse pastel red. CREA 25 °C, 7 days: Weak growth, acid production absent.

Micromorphology: Conidiophores biverticillate; stipes smooth-walled, 170–300 × 2.8–4.2 μm; metulae divergent, 3–6, 7–11.5 × 3–4.5 μm; phialides ampulliform, tapering to a very thin neck, 3–6 per metulae, 7.5–12.5 × 3–4 μm; conidia rough-walled, globose to subglobose, 2–3.3 × 2–3 μm.

Extrolites: Talaromyces purgamentorum produces a dibenzofuran, penicillide, purpactin A, a shamixanthone and a violaceol. The dibenzofuran had the same UV spectrum as karnatakafurans A and B (Manniche et al. 2004), but was more apolar. Penicillide and purpactins (also called vermixocins) are related extrolites that have been isolated from several *Talaromyces* species, including *T. derxii*, *T. purpurogenus* and *T. flavus* (Sassa et al. 1974; Suzuki et al. 1991; Proksa et al. 1992). These compounds have very high levels of bioactivity, and are inhibitors of acyl-CoA:cholesterol acyltransferases and calpain (Tomoda et al. 1991; Chung et al. 1998).

Acknowledgments This research was supported in part by NWO-WOTRO grants 895.100.014 and WB 84-525. Aida Vasco received grants from The Netherlands Fellowship Programmes (NFP) of the Netherlands organization for international cooperation in higher education (NUFFIC), The Faculty for the Future of Schlumberger Foundation (FFTF Grant 2011–2013) and The International Foundation of Science (IFS Grant D/5052–1, 2011-2-13f). Further financial support from the Studienstiftung Mykologie and the CBS-KNAW is greatly appreciated. Logistical support and collection permission was given by Tropenbos Colombia, and we thank Dr. Carlos Rodríguez for this. Uwe Braun is thanked for his advice on the new species names. Finally, we want to thank the indigenous people and the workers in the Parque Natural Nacional Amacayacu, Araracuara and Meta for their willingness to collaborate in this study.

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